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Breeding biology, morphometrics, and population dynamics of *Sylvia* warblers in the Eastern Baltic

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Between 1959 and 1995 members of the Biological Station Rybachy have studied on the Courish Spit of the Baltic Sea, among others, five *Sylvia* species: *S. nisoria, S. curruca, S. commums, S. borin,* and *S. atricapilla.* In this paper data are presented on the timing of migration and breeding, body size and mass, habitat and breeding density, position of nests, egg size and mass, incubation behaviour and incubation patches, breeding success, age structure of populations, mortality and longevity, and on population dynamics. Studies of bird population dynamics, based on trapping figures of migrating and breeding birds and on the numbers of nests found, showed that all these three parameters yield the same pattern of population changes. In 1974-1990 the numbers of the Barred Warbler dropped dramatically with the local population becoming extinct, Blackcap numbers significantly increased, and numbers of the Lesser Whitethroat remained stable.

Key words: Barred Warbler, Blackcap, Garden Warbler, Lesser Whitethroat, Whitethroat, age structure, breeding, migration, morphometrics, number dynamics, survival.

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1. Introduction

Among *Sylvia* warblers five species may be considered most numerous and widely distributed: Barred Warbler *Sylvia nisoria* (Bechstein, 1795), Lesser Whitethroat *Sylvia curruca* (Linnaeus, 1758), Whitethroat *Sylvia commums* Latham, 1787, Garden Warbler *Sylvia borin* (Boddaert, 1783), and Blackcap *Sylvia atricapilla* (Linnaeus, 1758). Data on their distribution, ecology, and breeding biology are presented in large handbooks of Palaearctic birds (Cramp et al. 1992, Glutz von Blotzheim & Bauer 1991), in regional reviews (Korelov 1972, Zatsepina 1978, Malchevsky & Pukinsky 1983, Kostin 1983, Levin & Gubin 1985, etc.), in monographic works (Siefke 1962, Schmidt 1981, Berthold et al. 1990), and in a large number of journal papers.

On the Courish Spit all five species were common in 1960s-1980s both during breeding period and during passage. Data on their numbers, timing of migration and breeding, and on various aspects of breeding biology were published by the researchers from the Biological Station Rybachy (Belopolsky & Odintsova 1969, Yefremov & Payevsky 1973, Vinogradova 1981, 1983, 1986, 1988, Payevsky 1973, 1985a, 1991, 1992, Sokolov 1991a, 1991b, Sokolov et al. 1998). Our studies showed that numbers of warblers were subject to considerable changes over these years. This inspired interest in the details of their population dynamics and their breeding success.

Since 1970s, many papers were published dealing with dynamics of avian populations on the basis of trapping figures (Berthold 1972, Busse 1973, Lipsberg & Rute 1974, Hjort & Lindholm 1978, Svensson 1978, Dolnik & Payevsky 1979, Lindholm et al. 1983, Payevsky 1985a, 1990, Busse & Cofta 1986, Berthold et al. 1986, Hjort & Pettersson 1986, Baumanis 1990, Sokolov 1990b, Busse & Marova 1993, Busse 1994, etc.). This interest was caused by a dramatic decline in a number of European species (especially in birds of prey and in insectivorous birds) that was to a large extent caused by use of pesticides and insecticides in agriculture and forestry (Ramad 1981). The validity of trapping figures as abundance estimates was supported by similar trends from different European sites, and in several cases by similar trends shown by populations of local breeders and passage migrants. The majority of ornithologists agreed that in order to use trapping figures for estimating numbers it is required (a) to use the same standard trapping method at the same site; (b) to keep the trapping season constant; (c) to analyse long-term trends on the basis of long data sets.

A way to verily the validity of trapping figures as population estimates is to compare them with counts of migrants and with surveys of breeding populations (Svensson 1978, Svensson et al. 1986). It was shown that trapping yields more representative data than do visual counts. It is possible to compare trapping figures with other count methods although annual counts of nests found in a fixed long-term study of a population have not been compared.

The aim of this paper is to present the data of 37-year study of five warbler species by members of the Biological Station Rybachy. All data on migration, breeding, age structure and population dynamics were re-analysed. A special attention was paid to the question whether any population parameters changed along the study period in relation to the change in numbers. All data were incorporated in this analysis, including those previously published in Russian.

2. Study site, material and methods

2.1. Study site

The study was conducted in the Kaliningrad Region of Russia (former Ostpreußen, Eastern Prussia) on the Courish Spit (Fig. 1) which is a narrow sandy strip oriented along the SW-NE axis, dividing the Courish Lagoon from the Baltic[1]. The spit is 97 km long and 0.5 to 3.8 km wide. The main dune chain follows the eastern (lagoon) coast, with the highest point 68 m a.s.l.. Along the western (sea) coast runs a sandy swell up to 8 m high, man-made but partly eroded. During formation the spit incorporated two islands (the village of Rybachy is situated on one) where soil is loamy, not sandy like the rest of the spit. In the early 17th century natural canopy covered 75% of the area, and in the early 19th century only 10%. Dunes moved on average 3-12 m per year, and the western coast retreated on average 1.5 m a year (Paul 1944 in; Nitsenko 1970). The struggle against wind erosion started in early 19th century by planting Mountain Pines *Pinus montana*, Lyme-grass *Elymus arenanus* and Marram Grass *Ammophila arenaria.* Later (mainly since 1950s) Scots Pines *Pinus silvestris* and Silver Willow *Salix acutifolia* were planted, on the pure sand it was Giant Lyme-grass *Elymus giganteus* (Nitsenko 1970).

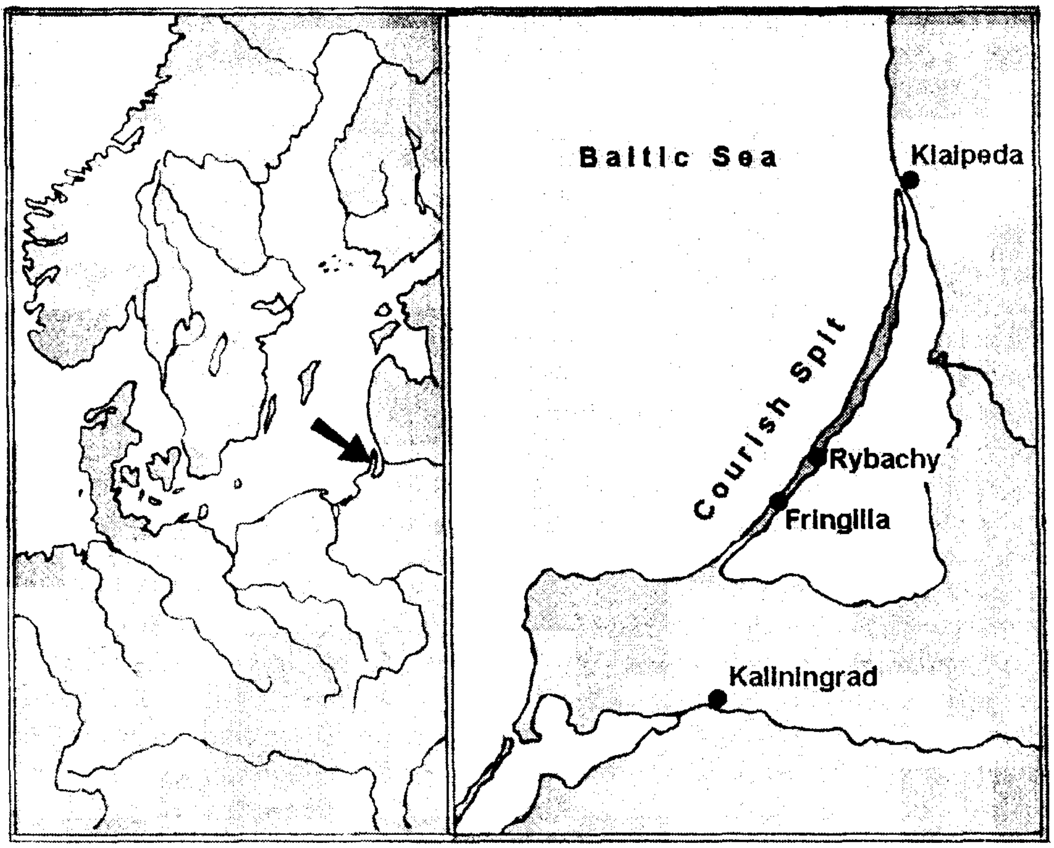

Figure 1. The Courish Spit. Location of study site "Fringilla".

[1] Names of the spit found in literature vary as a result of recent political changes, and of different translations and transliterations: in German Kurische Nehrung, in Lithuanian Kureiu Nerija, Kursiu Neringa, in English Curonian Spit, Courish Spit, Kursh Spit, Kurshskaya Spit, in Russian Kurshskaya kosa, Kurskaya kosa.

A pronounced habitat change may be recorded along the E-W transect, from bare sand dunes through sand with young willows and pine plantations to patches of deciduous and mixed coniferous - broad-leaved forest. The forest consists to a large extent of Scots and Mountain pine. Over the last 30 years the height of the pine plantations has grown from one to 8-10 m, pine forest incorporating and destroying many small patches of scrub. Natural stands are of Birch *Betula pendula* and Aspen *Populus tremula* forests. Herbage in forest patches includes Cow-wheat *Melampyrum pratense.* Hedge Bedstraw *Galium erectum,* Perforate St.John's Wort *Hypericum perforatum,* Common Bent *Agrostis capillaris* and Wild Strawberry *Fragaria vesca.* In low places Alder *Ainus glutinosa* groves occur with herbage of Common Nettle *Urtica dioica* and Bracken *Pteridium aquilinum.* Among shrubs Red Currant *Ribes rubrum* and Dewberry *Rubus caesitis* are very common, Common Juniper *Juniperus communis* and Barberry *Berberis vulgaris* occur regularly. Spruce forest occupy a small area and includes Common Spruce *Picea abies* and Canadian Spruce *P. canadensis.* In open places sand plants occur: Grey Hair-grass *Corynephorus canescens,* Sheeps-bit *Josione montana* and Sand Milk-vetch *Astragalus arenarius.* Only near Rybachy are there true meadows and small swamp meadows, natural deciduous forests with Small-leaved Lime *Tilia cordata.* Hornbeam *Carpinus betulus* and Pedunculate Oak *Quercus robur,* and also small patches of old spruce and pine forests with Wood Sorrel and Bilberry *(Oxalis* sp., *Vaccinium myrtilis)* group. A total of over 600 plant species occurs on the Courish Spit, many of them are introduced from Asia, the Alps, the Caucasus, the Crimea and from North America (Nitsenko 1970).

Climatic conditions on the Courish Spit differ from those on the neighbouring mainland: in spring it is colder and more humid on the spit, in summer cooler, and in autumn warmer. Phonological events are about one week retarded compared to the mainland. Mean air temperatures in May, July, and September are 12.0, 17.3 and 12.4 °C, respectively. In summer enormous numbers of chironomids (nudges) emerge from the Courish Lagoon and are taken by all passerines.

The Courish Spit is a flyway for mass migration of many bird species, primarily passerines (hundreds of thousands of individuals per day). That is why the first ever ornithological station *Vogelwarte Rossitten* was founded at Rybachy (Rossitten) in 1901 and performed research until 1944. In 1956 ornithological research here was recommenced by the Biological Station Rybachy of the Zoological Institute, Russian Academy of Sciences.

The study of avian breeding biology, incl. *Sylvia* warblers, was conducted at several sites on the spit, but most data concerning nests checked on the regular basis refer to the area around the field site "Fringilla", 12 km to the S of Rybachy at a site typical of the habitat of the Courish Spit (55°08' N, 20°42' E). With the example of the most numerous of our target species, Chaffinch *Fringilla coelebs*, it has been shown that monitoring of breeding populations of passerines was effective at the 4-km strip, 2 km to the NE and SW from "Fringilla". This area appeared satisfactory for the study of population parameters with an overall area for all habitats suitable for breeding woodland birds of about 2.5 km^2. This area of forest has been cleared twice, in 1975 and 1984. Apart from Scots Pine, also Brier, Barberry, Juniper and Mountain Pine, which are very attractive for all *Sylvia* warblers, were cleared through a misunderstanding.

2.2. Material and methods

Trapping has been conducted by the Biological Station Rybachy since 1957 at various sites along the spit. In this paper only data from main trapping site "Fringilla" are considered. Birds here were trapped in stationary Rybachy-type traps, in summer also in several mist nets. Rybachy-type traps resemble Heligoland traps but differ by non-rigid construction, absence of luring sites (water or food) and large size: the entrance is 20-30 m wide and 12-15 m hight (for detailed description s. Dolnik & Payevsky 1976). Annual trapping is conducted 24 h a day between April and November. The bulk of captures occur during spring and autumn migration. In summer when usually two traps are in operation local breeding birds are captured. Birds are not afraid of traps, not infrequently they breed near them (or even in the foreground of the inside). Many individuals are trapped repeatedly, e.g. a male Lesser Whitethroat which was ringed as a first-year and retrapped 18 times during subsequent eight years by all traps. Thus, a part of breeding population is regularly controlled.

Over the period 1959-1994 in all traps and mist nets 25,120 individuals of the five *Sylvia* species were trapped at "Fringilla". On May 28, 1992, we also trapped a female Subalpine Warbler *Sylvia cantillans* (Pallas, 1764) (Loskot et al. 1999). Numbers of first captures and retraps are presented in Tab. 1.

Table 1. Numbers of warblers trapped and recaptured at "Fringilla" by all traps and nets.

Species	Total trapped in 1959-1994	Yearly trapped		Number recaptured in 1959-1994 including birds ringed as nestlings
		maximum	mean	
S. atricapilla	3826	285	106	206
S. borin	6299	603	175	184
S. communis	3754	239	104	114
S. curruca	8932	501	248	1926
S. nisoria	2309	210	64*	702

Note: * Mean for 1959-1974 is 109, mean for 1975-1994 is 28.

Over the study period a varying number of researchers were collecting material on breeding biology. In 1974-1990 the data on open breeders were recorded in the journal "NEST" following a standardised format: nest number, bird species, site, habitat, nest height and species of supporting plant, finding date and nest contents, repeat visits and nest contents, fate of the nest (breeding success or numbers fledged or disaster such as predation), ring numbers of ringed nestlings. Every observer had his numbers for nests, which excluded the possibility of double recording.

In this paper the data for 1974-1990 are taken from "NEST" journals, and data for 1959-1973 and 1991-1995 from personal records of the author. As in 1974-1990 the number of recorded nests was much higher due to better coverage, the analysis of population trends by comparing numbers of nests found and trapping figures is restricted to this period.

Sample sizes are shown in tables and figures. From trapped birds two measurements were taken: wing length (maximum chord) to the nearest 1 mm, and body mass to the nearest 0.1 g. Eggs, nestlings and nests were weighed and measured to the nearest 0.01. Since 1972 birds have been aged and sexed after Svensson (1970), techniques were subsequently checked and refined by us (Vinogradova et al. 1976).

Breeding success was estimated by two methods. The first method is a traditional one, the ratio of fledglings to the number of eggs laid. Though, in the majority of cases not fledglings but ringed nestlings at the age of 7-12 days were recorded. The second technique is a modified Mayfield (1975) method. Its purpose is to estimate the daily rate of egg and nestling losses. The modification proposed by the author (Payevsky 1985b) is to use as a calculation unit not a nest, but an individual, an egg or a nestling. The rate of daily loss of eggs (q_e) and of nestlings (q_p) is calculated as follows:

$$q_e\text{-}\Sigma\, d_e/\, \Sigma t{\cdot}n.; \qquad q_p=\Sigma d_p/\Sigma t{\cdot}n_p$$

n_e being the number of eggs, n_p the number of nestlings in a nest, $\mathbf{d_e}$ the number of lost (not hatched) eggs, d_p the number of dead nestlings, t length of risk in days. Survival probability of an egg s_e is $\mathbf{(}1 - q_e)^{le}$, and survival probability of a nestling s_p is $\mathbf{(}1 - q_p)^{lp}$, le being incubation time, and lp length of staying in the nest. Probability of surviving from a laid egg to a ledged bird is s_e-s_p.

With migration still in process as local individuals start to breed, the discrimination of local breeders from passage birds may be difficult. Time intervals for a high probability of only local birds trapped were defined after Sokolov (1991b): Periods of trapping resulting in the highest percentage of retraps in subsequent years were found. In all juvenile *Sylvia* warblers this period was restricted to the first 10-day period of July to the first 10-day period of August, and for adults it appeared to be species-specific. In the Blackcap it lasted from early June (in 1987 from mid June) until early August, in the Garden Warbler from mid June until early August, in the Whitethroat from mid June until early

August, in the Lesser Whitethroat from late May (in 1987 from early June) until early July, in the Barred Warbler from late May until mid August. The shift in 1987 was caused by a very cold spring which delayed arrival.

3. Results

3.1. Timing of migration and breeding

Average dates of main summer events are shown in Tab. 2. Inter-specific variation in the timing of arrival and departure is clear. Pair-wise comparison of average arrival dates showed significant differences (t-value varying from 3.5 to 11.2; $p<0.01$ and $p<0.001$), except for the pair Blackcap - Lesser Whitethroat which showed no significant difference. Departure dates show significant differences in all cases ($p<0.001$).

The Blackcap spends most time in the breeding area (earliest arrival, latest departure), the Barred Warbler spends least time (latest arrival, earliest departure). The Lesser Whitethroat arrives as early as the Blackcap but departs on average a month earlier. The Whitethroat and the Garden Warbler are intermediate in this respect, but some Garden Warblers remain until last days of October, related to a shift to fruit diet which is observed also in the Blackcap on the Courish Spit. In general, the length of stay in the area of breeding (including post-fledging), calculated on the basis of first and last captures, is for the Blackcap on average 178 days, 153 days for the Garden Warbler, 149 days for the Lesser Whitethroat, 136 days for the Whitethroat and only 100 days for the Barred Warbler. The general pattern of warbler movements is presented in Fig. 2. The direction of autumn migration is SW (towards Italy) in the Garden Warbler, and SSE (towards eastern Mediterranean) in the Blackcap and Barred Warbler, based on ringing recoveries (Payevsky 1973).

The analysis of year-to-year variation in the timing of spring migration on the Courish Spit showed a significant negative relationship between May ambient temperature and the timing of migration in the Blackcap and Lesser Whitethroat, higher temperatures being associated with earlier migration (Sokolov et al. 1998). No such relationship was found in the Whitethroat and Garden Warbler.

Table 2. Timing of migration and breeding of *Sylvia* warblers, 1959-1995.

Indexes	***S. atricapilla***	***S. borin***	***S. communis***	***S. curruca***	***S. nisoria***
First bird trapped in spring*					
range	14 Apr. - 10 May	5 May - 19 May	*25* Apr. - 14 May	14 Apr.-11 May	8 May - 26 May
median	30 April	12 May	4 May	1 May	18 May
Timing of spring migration					
range	13 May - 29 May	20 May - 4 Jun.	18 May-31 May	11 May-31 May	28 May-09 Jun.
First egg laid					
N	257	289	38	421	325
earliest (inter-annual range)	15 May - 9 Jun.	23 May - 9 Jun.	-	10 May - 8 Jun.	22 May - 7 Jun.
overall range	15 May -10 Jul.	23 May - 13Jul.	25 May - 29 Jun.	10 May-13 Jul.	22 May - 27 Jun.
overall median	4 June	8 June	12 June	30 May	5 June
First juvenile trapped					
inter-annual range	7 Jul. – 16 Aug.	6 Jul. – 17 Aug.	6 Jul. - 19 Aug.	25 Jun.-24 Jul.	6 Jul. – 26 Jul.
median	23 July	24 July	24 July	8 July	15 July
Last bird trapped in autumn*					
inter-annual range	22 Sep. - 17 Nov.	13 Sep. - 28 Oct.	22 Aug. - 3 Oct.	4 Sep. - 22 Oct.	29 Jul. – 26 Sep.
median	24 October	12 October	17 September	26 September	25 August

Note: * local breeders and passage migrants pooled.

Mean laying dates in *Sylvia* warblers, in contrast to arrival dates, showed nearly no inter-specific variation (Tab. 2). Non-parametric Friedman's analysis of variance did not show significant difference between mean dates of laying first egg in five species $\chi^2 = 8.27$, n.s.), though in the Lesser Whitethroat laying occurred significantly earlier than in the Whitethroat, $p<0.05$. Thus suggests inter-specific variation in the time elapsed between arrival and commencement of breeding. Indeed, this interval varies broadly, from 19 days in the Barred Warbler to 39 days in the Whitethroat (27 days in the Garden Warbler, 29 days in the Lesser Whitetbroat, 37 days in the Blackcap).

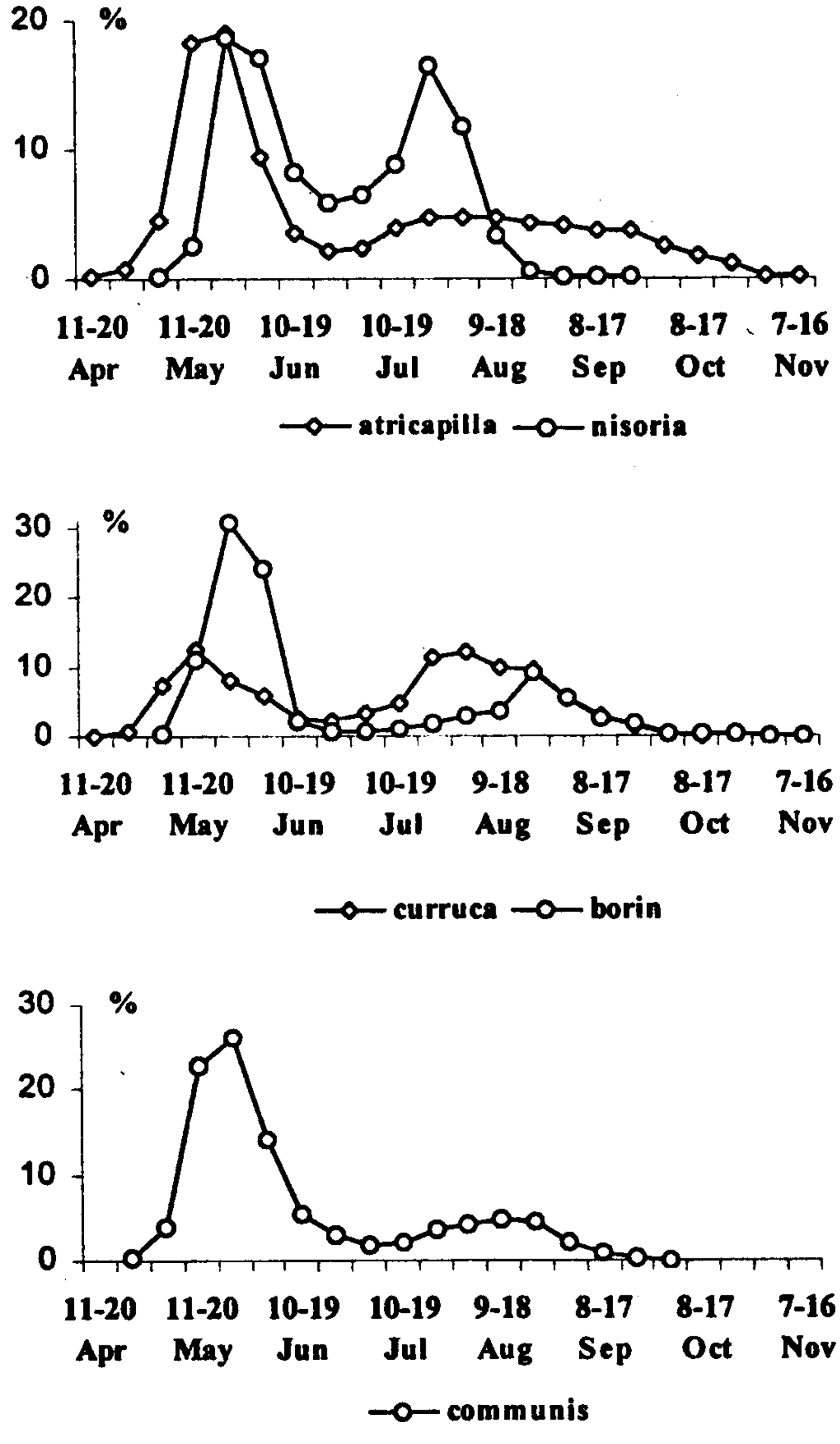

Figure 2. Timing and dynamics of movements of *Sylvia* warblers as shown by trapping data.

Inter-specific variation in laying and hatching dates is negligible, but inter-annual variation is significant. As shown elsewhere (Sokolov & Payevsky 1998), high ambient temperature in spring is related to early hatching (a significant negative correlation was found with April temperature in the Lesser Whitethroat, with May temperature in the Garden and Barred Warbler, and with June temperature only in the Whitethroat). Over the whole study period the earliest laying of the first egg was recorded in the Blackcap and Garden Warbler in 1990, and the latest one in 1987 in all *Sylvia* warblers (as with many other species).

Inter-specific variation in the average trapping dates of first juveniles is small (Tab. 2). Only in the Lesser Whitethroat first juveniles appear significantly earlier than in other species ($p<0,05$), which corresponds to the earlier laying. Elsewhere we showed that higher spring temperature is associated with early first traps of juveniles in all *Sylvia* warblers (Sokolov & Payevsky 1998). Spearman rank correlation coefficient showed significant negative relationship between first captures and April and May temperatures, and no relationship with June temperature.

Table 3. Wing length (mm) and body weight (g) of trapped warblers in different years (adult and second-year birds in April, May, and June).

	n	**range mean ± SE**		**n**	**range**	**mean ± SE**
S. atricapilla males						
1967 - 1974	185	72 - 81	76.4 ± 0.1	178	13.8 - 22.8	17.6 ± 0.1
1990 - 1994	207	71 - 81	76.1 ± 0.1	207	14.5 - 22.2	17.9 ± O.I
females						
1967 - 1974	163	71 - 81	76.0 ± 0.2	157	14.6 - 22.7	17.8 ± 0.1
1990 - 1994	186	72 - 81	76.2 ± 0.1	186	15.6 - 24.2	18.9 ± 0.1
S. borin						
1967 - 1974	517	74 - 85	79.5 ± 0.1	448	14.9 - 23.5	18.8 ± 0.1
1990 - 1994	344	73 - 85	79.8 ± 0.1	344	15.6 - 24.9	19.1 ± 0.1
S. communis males						
1967 - 1974	146	69 - 78	73.4 ± 0.2	107	12.4 - 18.0	14.3 ± 0.1
1990 - 1994	165	68 - 81	73.6 ± 0.1	165	11.5 - 17.7	14.9 ± 0.1
females						
1967 - 1974	120	67 - 76	71.6 ± 0.2	96	12.5 - 19.1	14.6 ± 0.1
1990 - 1994	133	68 - 77	72.3 ± 0.1	133	13.0 - 19.0	15.1 ± 0.1
S. curruca						
1967 - 1974	286	58 - 72	65.1 ± 0.2	162	10.1 - 14.2	11.7 ±0.1
1990 - 1994	408	61 - 72	65.4 ± 0.1	408	8.6 - 15.4	11.6 ± 0.1
S. nisoria males						
1967 - 1974	217	83 - 93	88.0 ± 0.1	204	20.1 - 28.7	23.8 ± 0.1
1987 - 1994	28	84 - 91	87.8 ± 0.4	28	20.6 - 26.8	23.9 ± 0.4
females						
1967 - 1974	143	80 - 91	87.4 ± 0.2	136	21.1 - 28.9	24.1 ± 0.1
1987 - 1994	33	82 - 90	85.9 ± 0.3	33	20.5 - 27.3	24.2 ± 0.3

3.2. Body size and mass of adult birds

As all trapped birds were measured and weighed, it is possible to compare measurements between years. Wing length and body mass were compared over two periods divided by a gap of 15 years: 1967-1974 (mean over eight years) and 1990-1994 (mean over five years). Only for the Barred Warbler the second interval had to be eight years (1987-1994) due to dramatic decline of numbers. When comparing body masses they were not corrected for wing length, as the interest was for the general condition of birds, including fat reserves. One would expect that rise and decline of populations could be associated with physical parameters of birds, e.g. with changes in measurements. Difference in both size and mass was very slight (Tab. 3). In only two cases were obvious shifts recorded: mean mass of female Blackcaps increased by 1.1 g (t = 6.25, p<0.001), and wing length of female Barred Warblers declined by 1.5 mm (t = 4.11, p<0.001). Some other shifts were also significant (p<0.05 and p<0.01): increase of wing length in Garden Warblers and in female Whitethroats and mass increase in Garden Warblers and in Whitethroats.

3.3. Habitat preferences and breeding density

In most cases breeding territories of different warbler species occupy the same habitats. The most densely populated habitats are mixed forests with shrubs of Red Currant and Dewberry and scrubby edges of mature forests. Most nests of Garden and Barred Warblers and Blackcaps were found at such sites. Only Lesser Whitethroats can inhabit core parts of young Scots pine plantations, only Whitethroats can breed in low willow scrub on the dunes of the Baltic coast. Most territories of Barred Warblers included open habitats: small clearances in mountain pine stands, in scrubby forest edges or in the shrubs in mixed forest. At the same sites Red-backed Shrike *Lanius collurio* Linnaeus, 1758 used to breed in the 1960s and 1970s, breeding territories of these species frequently overlapping. Both species suffered a dramatic decline in the 1980s and disappeared from our study area practically simultaneously.

Studies of the habitat selection and territorial behaviour of *Sylvia* warblers on the Courish Spit were done by Vinogradova (1981, 1983, 1986, 1988). These studies showed that isolated from other species are those individuals of the Garden Warbler that breed in the shrubs in mature birch forests. In all other habitats two to five species co-exist. The Barred Warbler inhabited most varying habitats. Blackcaps and Garden Warblers compete for territory, competition being acute due to different timing of arrival and similar habitat selection.

Table 4. Plant species supporting nests of *Sylvia* warblers (percentage).

Plant species	*S. atricapilla* n = 384	*S. borin* n = 344	*S. communis* n = 63	*S. curruca* n = 657	*S. nisoria* n = 566
Common Spruce, *Picea abies* Karst.	6.2	1.5	-	3.3	2.7
Canadian Spruce *Picea canadensis* Sarg.	0.5	-	-	0.6	-
Common Larch, *Lam decidua* Mill.	-	-	-	0.2	0.7
Scotch Pine, *Pinus siluestris* L.	0.3	1.2	-	29.2	13.3
Mountain Pine, *Pinus montanus mughus* (Mill.)	0.8	1.5	-	21.6	18.0
Austrian Pine, *Pinus nigra* Arn.	-	-	-	-	0.5
Crimean Pine, *Pinus pallasiana* Lamb.	-	-	-	3.7	0.3
Common Juniper, *Juniperus communis* L.	1.0	2.8	-	37.0	5.3
Silver Willow, *Salix acutifolia* Willd., and Violet Willow, *S. daphnoides* Vill.	-	1.2	11.0	-	1.2
European Aspen, *Populus tremula* L.	0.5	1.7	-	-	0.2
White Birch, *Betula pubescens* Ehrh. and Weeping Birch, *B. pendula* Roth.	0.3	0.6	-	0.3	2.3
Black Alder, *Ainus glutinosa* (L.)	1.6	1.5	1.6	-	0.2
Smooth Elm, *Ulmus laevis* Pall.	0.3	-	-	-	-
Common Nettle, *Urtica dioica* L.	0.8	3.8	-	-	0.2
Common Barberry, *Berberis vulgaris* L.	1.3	1.5	3.2	1.6	6.9
Trailing Mahonia, *Mahonia aquifolium* Nutt.	-	-	-	-	-
Red Currant, *Ribes rubrum* L.	71.4	39.5	3.2	0.3	18.7
Mountain Ash, *Sorbus aucuparia* L.	1.3	0.8	-	-	-
English Hawthorn, *Crataegus oxyacantha L.*	0.3	-	-	-	1.1
Red Raspberry, *Rubus idaeus* L.	2.1	1.7	-	-	1Л
Dewberry, *Rubus caesius* L.	6.8	36.6	76.2	1.5	23.3
Ramanas Rose, Rosa *rugosa* Thumb., and Cinnamon rose, *Rosa cinnamomea* L.	0.3	0.6	1.6	0.2	3.2

Sea Pea, *Lathyrus marttimus* (L.)	-	-	1.6	-	-
Sallow Thorn, *Frangula ainus* Mill.	-	0.6	-	-	-
Red Elder, *Sambucus racemosa* L.	2.9	-	-	-	-
Common Snowball, *Viburnum opulus* L.	0.3	0.3	-	-	0.3
Common Snowberry, *Symphoricarpus migaris* L.	-	-	-	0.2	0.2
Dry brushwood	1.0	2.3	1.6	0.3	0.3

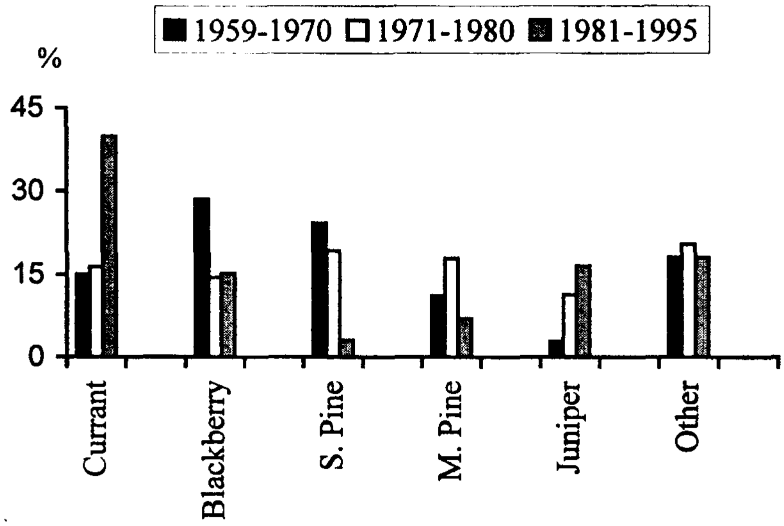

Figure 3. Inter-annual variation in the distribution of warbler nests on different species of vegetation.

Breeding density is studied most thoroughly in the Barred Warbler (Vinogradova 1981, 1986, 1988). In 1974-1978 it was 16-26, on average 20 pairs·km^{-2}, then a dramatic decline was recorded. Between 1982-1986 the breeding density decreased to 4, and then to 0.4 pairs·km^{-2}. The last Barred Warbler nest was found in the study area in 1986 until in 1997 when two nests were found (L. Sokolov, V. Yefremov, pers. comm.). In favourable years in the most favoured area of 4 ha breeding density reached 3 pairs·ha^{-1}. In 1980 in six breeding pairs areas of breeding territories were 700 to 1250 m^2, on average 1050 m^2. Combined breeding density of the Blackcap and the Garden Warbler reached 0.94 pairs·ha^{-1} in the most densely populated patches, at the rest of the study area it did not exceed 40 pairs·km^{-2} in any of these species separately. Lesser Whitethroat's breeding density was estimated only at several most preferred sites where it reached 2 pairs·ha^{-1}, in the study area it averaged 60 pairs·km^{-2}. Data on the breeding of the Whitethroat is much less comprehensive, which is caused by well-hidden nests and inconspicuous during incubation. It is not less abundant in summer as the Garden Warbler.

3.4. Position of nests

Sylvia warblers' nests were recorded on 28 different plant species (Tab. 4). Blackcaps favoured Red Currant ($\chi_1^2 = 18.3$, p<0.001), Garden Warblers equally Red Currant and Dewberry ($\chi_1^2 = 27.2$, p<0.001), Whitethroats selected Dewberry ($\chi_1^2 = 27.5$, p<0.001), Lesser Whitethroats favoured Juniper, Scots and Mountain Pine ($\chi_1^2 = 57.2$, p<0.001), Barred Warblers favoured Red Currant, Dewberry, Scots and Mountain Pine ($\chi_1^2 = 21.7$, p<0.001). Inter-annual variation in this respect was recorded. I analysed the data by non-parametric Friedman's test, dividing the study period into three intervals (1959-1970, 1971-1980, 1981-1995) and plants into six classes (Red Currant, Dewberry, Scots pine, Mountain Pine, Juniper, and 'other species'). Both factors, i.e. time interval and plants, varied broadly ($\chi_1^2 = 4.71$, n.s.). The overall pattern is presented in Fig. 3.

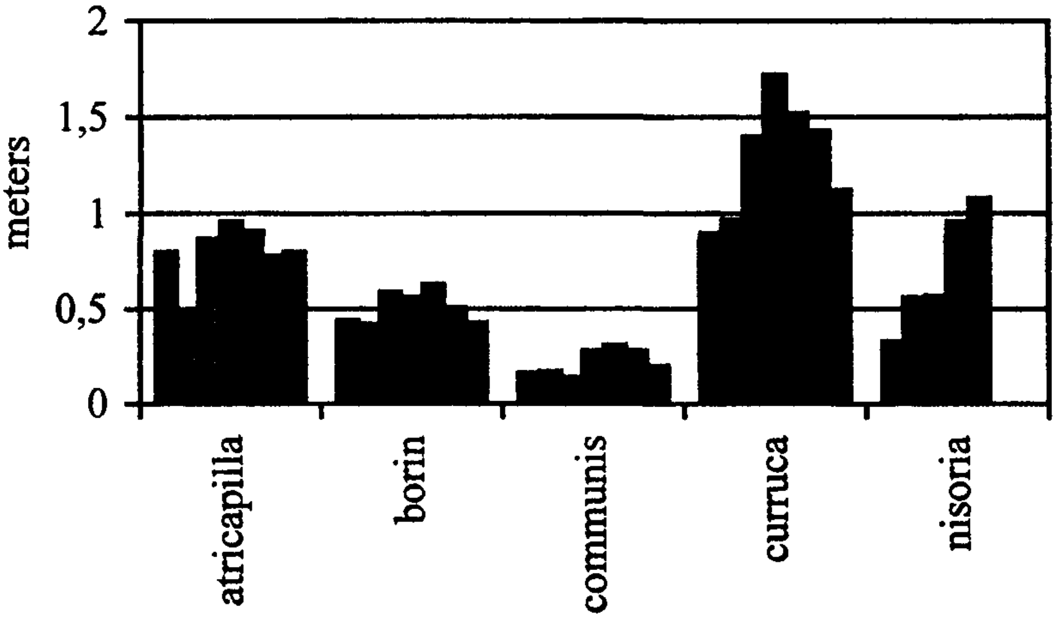

Figure 4. The height of nests location above the ground. Each column shows average height in different years, from the left, respectively: 1959-1964,1965-1970,1971-1975,1976-1980,1981-1985,1986-1990,1991-1995.

The proportion of all warbler nests on Red Currant increased in 1981-1995 compared to previous years (χ_1^2 - 9.8, p<0.01), this increase being significant in the Blackcap (χ_1^2 = 3.8, p<0.05) and in the Garden Warbler (χ_1^2 = 12.2, p<0.001). The proportion of warbler nests on Scots Pine declined in 1981-1995 compared to 1971-1980 (χ_1^2 = 11.6, p<0.001) and to 1959-1970 (χ_1^2 - 16.3, p<0.001), this shift being most obvious in the Lesser Whitethroat (χ_1^2 = 5.6, p<0.05; χ_1^2 = 14.3, p<0.001, respectively). A decreased tendency to build nests on Mountain Pine was recorded in 1981-1995 compared to 1971-1980 (χ_1^2 = 4.7, p<0.05), although in individual species this trend was not significant. Increased proportion of nests built on Juniper in 1981-1995 compared to previous years was recorded in the Lesser Whitethroat (χ_1^2 = 7.9, p<0.01) which uses this plant most frequently. No significant trends were recorded for other plant species.

Nest height over ground was analysed without reference to supporting plant species (Fig. 4). The two-way ANOVA showed that nest height was dependent on both bird species and year (F = 10.29, p<0.001). The highest average nest position was recorded in the Lesser Whitethroat (average 1.29 m, range 0.2 - 5.5 m), the lowest in the Whitethroat (average 0.22 m, range 0.05 - 0.6 m). The average was 0.80 m in the Blackcap (range 0.1 - 2.9 m); 0.51 m in the Garden Warbler (range 0.1 - 2.5 m), 0.70 in the Barred Warbler (range 0.1 - 2.5 m). Pair-wise comparison of nest height between species showed significant difference in all cases (p < 0.01; p < 0.001). A significant change of nest height over study years was recorded in two species: in the Barred Warbler it increased between 1959 and 1985 (r = 0.97, p < 0.01), in the Lesser Whitethroat was increasing between 1959 and 1980 (r = 0.97, p < 0.001) and decreasing between 1980 and 1995 (r = 0.98, p < 0.01).

Some data on the nest size in the Blackcap and the Garden Warbler are available. The following parameters were recorded in cm: H - height of a nest, h - cup depth, D - nest diameter, d - cup diameter. Blackcap (n = 14): H - 7.48, range 6.5 - 9.3; h - 3.90, range 3.3 -5.5; D - 9.84, range 9.3 - 10.6; d - 5.91, range 5.5 - 6.3. Garden Warbler (n = 12): H - 8.29, range 6.0 - 9.2; h - 5.48, range 5.0 - 6.2; D - 11.24, range 9.5 - 12.4; d - 6.30, range 6.0 - 7.0. Blackcap nests dried at 60°C weighed 5.03 g (range 3.94 - 7.21, n = 14), Garden Warbler nests 7.66 g (range 6.07 - 9.93; n = 8).

Over the study period several cases were recorded when exactly the same sites on the same red currant or juniper plant were used for building nests by the same warbler species in several years.

3.5. Egg size and mass

Egg biometrics is shown in Tab 5. Nestlings weighed immediately after hatching 1.94 ± 0.05 g in the Blackcap (range 1.58 - 2.25, n-18) and 1.24 ± 0.04 g in the Lesser Whitethroat (range 1.05-1.46, n = 12).

Weighing eggs on the day of laying (5 Blackcap clutches and 6 Garden Warbler clutches) showed a trend of increasing mass of subsequent eggs, but this trend was significant only in three Garden Warbler clutches (Spearman rank correlation r_s 0.90 to 1.00; $p<0.05$, $p<0.01$, $p=0.00$) and one Blackcap clutch ($r_s = 1.00$, $p = 0.00$). Nevertheless, the first egg always weighed less than the last egg in both species. In the Blackcap the first egg weighed 1.97 to 2.49, on average 2.22 g, the last egg weighed 2.12 to 2.56, on average 2.40 g, the difference being significant (sign test, $z = 1.88$, $p < 0.05$). In the Garden Warbler the first egg weighed 2.08 to 2.64, on average 2.29 g, the last egg 2.25 to 2.73, on average 2.56 g (sign test, $z = 2.04$, $p < 0.05$). A similar pattern was observed in the Icterine Warbler *Hippolais icterina* (Vieillot, 1817) on the Courish Spit (Payevsky 1987).

3.6. Incubation behaviour and incubation patches

The main results concerning incubation behaviour and stages of incubation patch have been published elsewhere (Yefremov & Payevsky 1973). Incubation was studied by observing individually marked pairs from hides.

Table 5. Size and weight of *Sylvia* warblers' eggs.

Species	Size, mm					Weight on the day of laying, g		
		length		width				
	n	range	mean ± SE	range	mean ± SE	n	range	mean ± SE
S. atricapilla	58	17.0 - 20.4	18.75 ±0.11	13.3 -15.8	14.46 ± 0.06	63	1.82 - 2.99	2.23 ± 0.03
S. borin	43	18.1-21.0	19.75 ± 0.68	13.4 -15.4	14.61 ± 0,09	52	2.08 - 2.73	2.37 ± 0.02
S. curruca	26	16.1 - 18.1	16.90 ± 0.12	11.0-14.1	12.73 ± 0.10	31	1.30 -1.57	1.43 ± 0.01

During the whole incubation period males are regularly singing in all species studied, although singing frequency is much lower later than at the beginning of breeding, or when starting a repeated breeding attempt after losing a nest. Thus, a very high singing frequency in a male Blackcap, apparently an unmated one, was recorded: he sang the complete song 62 times in 10 minutes after getting awake, i.e. he was singing practically non-stop. Singing frequency during incubation which is shared by both sexes is much lower, although at dawn it is still high. In all species except for the Lesser Whitethroat males sing a short abridged song before replacing a female at nest, this song being a part of the usual species-specific one. Females did not produce any calls (at least those perceivable by humans) when replacing a male at nest.

The results of observations are summarized in Tab. 6. In all five species only females stayed at nest at night. Length of female's stay at nest at night varies related to light conditions and the general rhythm of incubation. It comprises 5 to 8.6 hours without any significant inter-specific variation. The length of single incubation sessions is very variable in both sexes in all species. In the Lesser Whitethroat and in the Whitethroat overall male's stay at nest was increasing to the end of incubation. Male's behaviour at nest did not differ from female's (moving eggs, helping newly batched nestlings to get rid of shell fragments, feeding attempts minutes after hatching). In all species males participated in incubation and in warming nestlings, spending some time at nests (along with females) even with 6-day old nestlings. Both male and female Lesser Whitethroat and Barred Warblers when replacing a partner were bringing spider cocoons, which were used for lining of nest edges.

In three cases males stopped incubating after being trapped at nests. It had a limited impact on the total duration of incubation. Females compensated for the lack of incubation by males by prolonging incubation sessions (Barred Warbler), or by spending less time outside the nest (Blackcap), or both (Garden Warbler). Though these males did not incubate, they were still defending territory and warning females. Besides, the male Garden Warbler produced "replacement calls" in equal time intervals, after which the female left the nest.

Table 6. Share in incubation (minutes) of males and females.

Species	Number of nests	Nocturnal incubation by female		Duration of single incubation act at day-time				Average proportions (%) of 24h		
				female		male		female	male	nest off
		range	mean	range	mean	range	mean			
S. atricapilla	2	450 - 481	466	3-75	27.1	2-34	16.5	82.7	6.3	11.0
S. borin	2	400 - 410	405	5-47	17.0	4-19	9.1	78.4	5.0	16.6
S. communis	3	358-496	408	1-73	15.6	1-85	27.3	63.3	27.6	9.1
S. curruca	4	300-437	378	2-90	31.0	13-50	28.7	68.6	27.5	3.9
S. nisoria	4	380 - 518	428	1-57	14.6	1-32	12.3	69.7	26.6	10.4

As male *Sylvia* warblers commence building nests (at first several rudimentary cock-nests, then the true nest) before females arrive, males start to defend breeding territories very early, soon after arrival. In several warbler species females also participate in territory defending, this trait being especially obvious in some female Barred Warblers (Vinogradova 1986).

Males' participation in incubation (the mean proportion of a day when a male is incubating) was the same in the Barred Warbler, Whitethroat, and Lesser Whitethroat (26.6%, 27.6%, 27.5%, respectively, n.s.) and significantly higher ($p<0.001$) than in the Blackcap and Garden Warbler (6.3% and 5.0%, n.s.).

Incubation patches were recorded in males of every species, except for the Whitethroat. This is also confirmed by the data on trapped male Whitethroats. In not a single male Whitethroat was feather loss recorded, which is the first typical feature during formation of an incubation patch. Most developed patches are found in male Lesser Whitethroats and Barred Warblers. In males the patches were going through the same development as in females: (1) loss of flocci at the ventral apteria; (2) skin is getting vascularized and thick; (3) skin becomes swelling; (4) recovery stage.

In all regular incubation started after laying the fourth, less frequently the fifth egg. Duration of regular incubation until hatching was 11-12 days in the Blackcap and Garden Warbler; 11-12, sometimes 13 days in the Lesser Whitethroat; 12-13, once 14 days in the Barred Warbler. A female Barred Warbler was incubating a clutch of five eggs for at least 18 days, from June 11 until June 29, 1974. The male was never recorded at this nest. The eggs appeared to be dead and dry, when shaking their content was tapping; they may have never been fertilized. The egg laid first hatched in the Blackcap and Garden Warbler usually on the 15th day after laying, laid second - on the 14th etc., however, the hatching order did not necessarily exactly followed the laying order.

3.7. Whitethroat as Cuckoo host on the Courish Spit

Over the study period twice was a Cuckoo *Cuculus canorus* Linnaeus, 1758 host identified by the author. It was the Whitethroat. In a Whitethroat nest which was found on July 6, 1960, one egg out of four was slightly larger and paler. On July 17 a Cuckoo nestling was found in the nest, and three 3-days old Whitethroat nestlings, one of them still breathing, under the nest. When put back to the nest, this nestling was not removed by the Cuckoo for at least one hour. On July 11, 1987 a fledgling Cuckoo of the grey morph (with nearly no brown colour) was seen two km to the north of "Fringilla". The Cuckoo was fed by a Whitethroat. The fledgling was flying well, its host followed it, collecting insects *en route*. In the old Eastern Prussia 11 passerine species were recorded as Cuckoo hosts, most frequently the White Wagtail *Motacilla alba* Linnaeus, 1758, and also the Whitethroat and Barred Warbler (Tischler 1941).

3.8. Breeding success

3.8.1. Clutch size

In all species studied the maximal clutch size was 6 eggs, average size over the whole study period varied between 4.73 in the Blackcap and 5.13 in the Lesser Whitethroat. Clutch size of 6 eggs was recorded in 15 clutches of Blackcap (5.2%), 3 clutches of Garden Warbler (1.0%), 5 clutches of Whitethroat

(11.9%), 85 clutches of Lesser Whitethroat (19.6%), and in 19 clutches of Barred Warbler (5.4%).

I analysed the size of complete clutches during the breeding season over 5-day periods on the basis of known or calculated date of laying the last egg (Tab. 7). In the Blackcap, Barred Warbler and Lesser Whitethroat clutch size was decreasing during the breeding season. Despite of some variation, a negative correlation between clutch size and progression of season was significant in these species, in contrast to the non-significant relationship in the Garden Warbler.

Table 7. Variation of completed clutch size along the breeding season (pooled data for 1959-1995 for the five-days periods with at least 10 completed clutches).

Five-days periods	*S. atricapilla*		*S. borin*		*S. curruca*		*S. nisoria*	
	n	mean ± SE	n	mean ± SE	n	mean ± SE	n	mean ± SE
16 May - 20 May					12	5.50 ±0.15		
21 May - 25 May	23	4.91 ± 0.12			54	5.24 ± 0.09		
26 May - 30 May	29	5.03 ± 0.12	11	4.91 ± 0.09	73	5.32 ± 0.06		
31 May - 4 June	45	4.98 ± 0.05	28	5.04 ± 0.04	50	5.16 ± 0.06	59	4.91 ± 0.08
5 June - 9 June	23	5.00 ± 0.06	42	4.83 ± 0.06	38	5.17 ± 0.08	114	4.85 ± 0.05
10 June - 14 June	27	4.93 ± 0.09	48	4.71 ± 0.07	38	4.84 ± 0.11	116	4.87 ± 0.05
15 June-19 June	18	4.83 ± 0.15	39	4.79 ± 0.09	34	4.84 ± 0.11	20	4.70 ± 0.12
20 June-24 June	24	4.29 ± 0.14	23	4.57 ±0.11	18	4.61 ± 0.41	11	3.91 ± 0.31
25 June-29 June	11	3.91 ± 0.21	13	4.92 ± 0.08	18	4.50 ± 0.17		
30 June- 4 July					13	4.46 ± 0.28		
Coefficient of correlation		$r = -0.799$ $p < 0.05$		$r = -0.476$ n.s.		$r = -0.975$ $p < 0.001$		$r = -0.809$ $p = 0.097$

3.8.2. Hatching success

Partial losses were caused by embryonic mortality and by small fraction of unfertilised eggs. The size of clutches containing eggs that never hatched, did not differ from the average size of completed clutches in the population. The average number of not hatched eggs per completed clutch was 0.09 in the Whitethroat, 0.22 in the Barred Warbler, 0.23 in the Lesser Whitethroat, 0.30 in the Blackcap and 0.33 in the Garden Warbler. When not developing eggs were found in a clutch, their number varied between one and three. Proportion of eggs that were not developed among those survived to hatching, varied from 1.8% in the Whitethroat to 7.0% in the Garden Warbler.

The main reason of egg and nestling loss was predation. On the Courish Spit, marten, Common and Least Weasels, squirrel and stray cats were recorded as nest predators. In different years 50 to 98% of laid eggs survived to hatching in different species, on average 80-86% (Tab. 8).

Table 8. Summary of breeding performance of *Sylvia* warblers, 1959-1995.

Species	No. of nest found with eggs or nestlings	Complete clutch size			No. of eggs laid		Hatching success, %		Nestlings survived* as percent of eggs laid		Breeding success (%) calculated after Mayfield (1975)	
		n	yearly range of	overall mean±SE	Cont-rolled	Known fate	Yeariy range	Mean ± SE	Yearly range	Mean±SE	Yeariy range	Mean ± SE
S.atricapilla	322	287	4.33-5.17	4.73±0.04	1386	1203	53.8 - 97.8	78.6±1.6	39.1-94.3	72.5±1.6	31.8-91.5	59.7±0.7
S. borin	341	288	4.38-5.00	4.76±0.03	1459	1250	58.5 - 96.4	82.4±1.2	48.3-90.0	73.2±1.5	39.3-87.2	62.1±0.6
S. commu-	45	42	-	4.95±0.08	208	147	-	86.4±2.8	-	80.3±3.3	-	70.8±1.3
S.curruca	533	433	4.75-5.50	5.13±0.03	2412	1877	50.0 - 95.7	80.3±1.1	49.2-92.8	73.4±1.2	43.8-79.2	64.3±0.5
*S.nisoria***	371	355	4.54-5.13	4.90±0.05	1957	1400	65.0 - 92.9	80.9±1.3	50.0-90.1	74.9±1.4	34.2-86.0	64.6±0.6

Notes. * survived up to the age of at least 6-10 days; ** the last active nest of Barred Warbler was found in 1986, followed by two nests in 1997.

3.8.3. Overall breeding success and its inter-annual variation

Average values of clutch size, hatching success and nestling survival are presented in Tab. 8. Breeding success was very similar in all species, 60-70% after Mayfield (1975) method.

Variation of clutch size and breeding success was analysed separately in the 1960s, 1970s and 1980s (Tab. 9). In several cases these parameters varied significantly. In the Barred Warbler and Lesser Whitethroat clutches were larger in the 1960s than in the 1970s, and in the Blackcap larger in the 1980s than in the 1970s. Breeding success in the Blackcap was significantly higher in the 1980s than in the 1970s and 1990s, and in the Garden Warbler it was higher in 1960s than in 1970s and 1980s. Only in the Barred Warbler breeding success was higher in the 1970s than in the 1960s and similar to success in the 1980s.

Table 9. Variations of clutch size and breeding success in different years.

Species, years	Complete clutch size			Breeding success, % (after Mayfield)		
	n	mean ± SE	t-test	n	mean ± SE	t-test
			S. atricapilla			
1971-1980	44	4.59 ± 0.09		211	52.1 ± 1.5	
			2.2; p < 0.05			27.7; p < 0.01
1981-1990	195	4.82 ± 0.04		934	71.0 ± 0.6	
			0.0; n.s.			58.2; p < 0.001
1991-1995	33	4.82 ± 0.10		161	40.6 ± 0.7	
			S. borin			
1959-1973	35	4.77 ± 0.09		169	78.4 ± 1.4	
			0.2; n.s.			17.4; p < 0.001
1974-1980	56	4.79 ± 0.09		304	59.7 ± 1.2	
			0.5; n.s.			0.3; n.s.
1981-1990	183	4.73 ± 0.07		916	58.0 ± 0.7	
			S. curruca			
1960-1970	56	5.25 ± 0.07		328	66.5 ± 1.3	
			2.2; p < 0.05			2.4; n.s.
1971-1980	197	5.06 ± 0.06		1091	61.7 ± 0.8	
			1.9; n. s.			1.7; n.s.
1981-1990	169	5.20 ± 0.05		932	64.4 ± 0.7	
			S. nisoria			
1959-1970	72	4.96 ± 0.05		376	59.5 ± 1.2	
			2.2; p < 0.05			8.3; p < 0.01
1971-1970	252	4.83 ± 0.04		1408	67.6 ± 0.6	
			1.1; n.s.			0.1; n.s.
1981-1986	31	4.96 ± 0.09		173	67.0 ± 1.6	

3.9. Age structure, mortality and longevity

Population age structure was calculated in three species on the basis of retraps in years following ringing (Tab. 10). In spring and in summer before fledging one-year and two-year old birds comprised the bulk of the population (70-80%). For each thousand birds there are 32 individuals older than 5 years in the Barred Warbler, 16 ones in the Garden Warbler, and 24 ones in the Lesser Whitethroat. The method of composite life tables yields the following mean annual survival from the data presented in Tab. 10: 51.0% in the Barred Warbler, 41.4% in the Garden Warbler, 41.9% in the Lesser Whitethroat. Survival of the latter species was estimated elsewhere (Payevsky 1992) by two alternative methods: by composite life tables and by Jolly-Seber capture-recapture stochastic analysis, modification of Pollock (1981). The difference between results yielded by these methods was not significant (40.0% and 47.7%). No difference was found in annual survival rates for males (50.2%) and females (49.1%) of Barred Warbler using recaptures in 1967-1976 calculated by programme JOLLY (Payevsky et al. 1997).

Table 10. Age structure of *Sylvia* warblers populations calculated by means of recaptures*.

Age, years	Age structure, % ± SE		
	S. nisoria	*S. borin*	*S. curruca*
1	53.5 ± 2.0	60.1 ± 3.5	58.1 ± 2.2
2	22.0 ± 1.7	21.2 ± 2.9	22.8 ± 1.8
3	11.7 ± 1.3	10.1 ± 2.1	10.4 ± 1.3
4	6.5 ± 1.0	5.1 ± 1.6	4.6 ± 0.9
5	3.4 ± 0.7	2.0 ± 1.0	1.7 ± 0.6
6	1.5 ± 0.5	1.0 ± 0.7	1.0 ± 0.4
7	0.7 ± 0.3	0.5 ± 0.5	0.8 ± 0.4
8	0.5 ± 0.3	-	0.6 ± 0.3
9	0.2 ± 0.2	-	-

* Each bird recaptured during the years after the year of ringing was included in each age category before the its age (e.g. a bird recaptured on the third year after ringing as juvenile was included in the age category 1, 2 and 3). So by convention the numbers of populations are obtained as 596 birds for *S. nisoria,* 198 birds for *S. borin*, and 517 birds for *S. curruca.*

Maximum longevity of the Garden Warbler recorded on the Courish Spit is 7 years (one bird), in the Barred Warbler 9 years (one 9-year old male, two 8-year old males, three males and one female reached 7 years), in the Lesser Whitethroat 8 years (three males). The mean life expectation after reaching maturity is approx. 1 year 6 months in the Barred Warbler, and 1 year 3 months in both Garden Warbler and Lesser Whitethroat.

Population sex structure was estimated in the Blackcap on the basis of all captures on the Courish Spit in 1969-1988 (Payevsky 1993). Proportion of males is 56.6% ± 1.6% in spring and summer. 55.2% ± 1.7% in autumn.

Table 11. Population trends of *Sylvia* warblers in 1974-1990 by the coefficient of Kendall rank correlation *(v)* and by the coefficient of correlation of time-series (r). Significance levels: * p<0.05, ** p<0.01, *** p<0.001.

Indices			*S. atricapilla*	*S. borin*	*S. communis*	*S. curruca*	*S. nisoria*
Annual total		Range	42 - 285	66-603	44-239	177-493	4-159
		Mean	135	203	125	371	45
		τ	+ 0.415*	- 0.022	+ 0.272	+ 0.022	- 0.852***
		r	+ 0.543*	+0.208	+ 0.401	+ 0.157	- 0.842***
Local birds	Adults	Range	2-29	1-16	1-19	25-35	4-110
		Mean	11	7	11	39	29
		τ	+ 0.260	+ 0.243	+0.084	-0.111	- 0.739***
		r	+ 0.151	+ 0.410	+0.266	- 0.181	- 0.786**
	Juveniles	Range	1-80	1-40	2-26	35-268	0-46
		Mean	16	17	11	162	15
		τ	+ 0.622***	+ 0.537"	+ 0.463*	+ 0.044	- 0.682**
		r	+ 0.678**	+ 0.687"	+0.589*	+ 0.016	- 0.805***
	Nests	Range	4-73	8-57	0-11	5-99	0-66
		Mean	21	20	3	33	22
		τ	+ 0.736***	+ 0.543**	+ 0.393*	- 0.274	- 0.929***
		r	+ 0.711**	+ 0.634*	+ 0.494	-0.366	- 0.940***

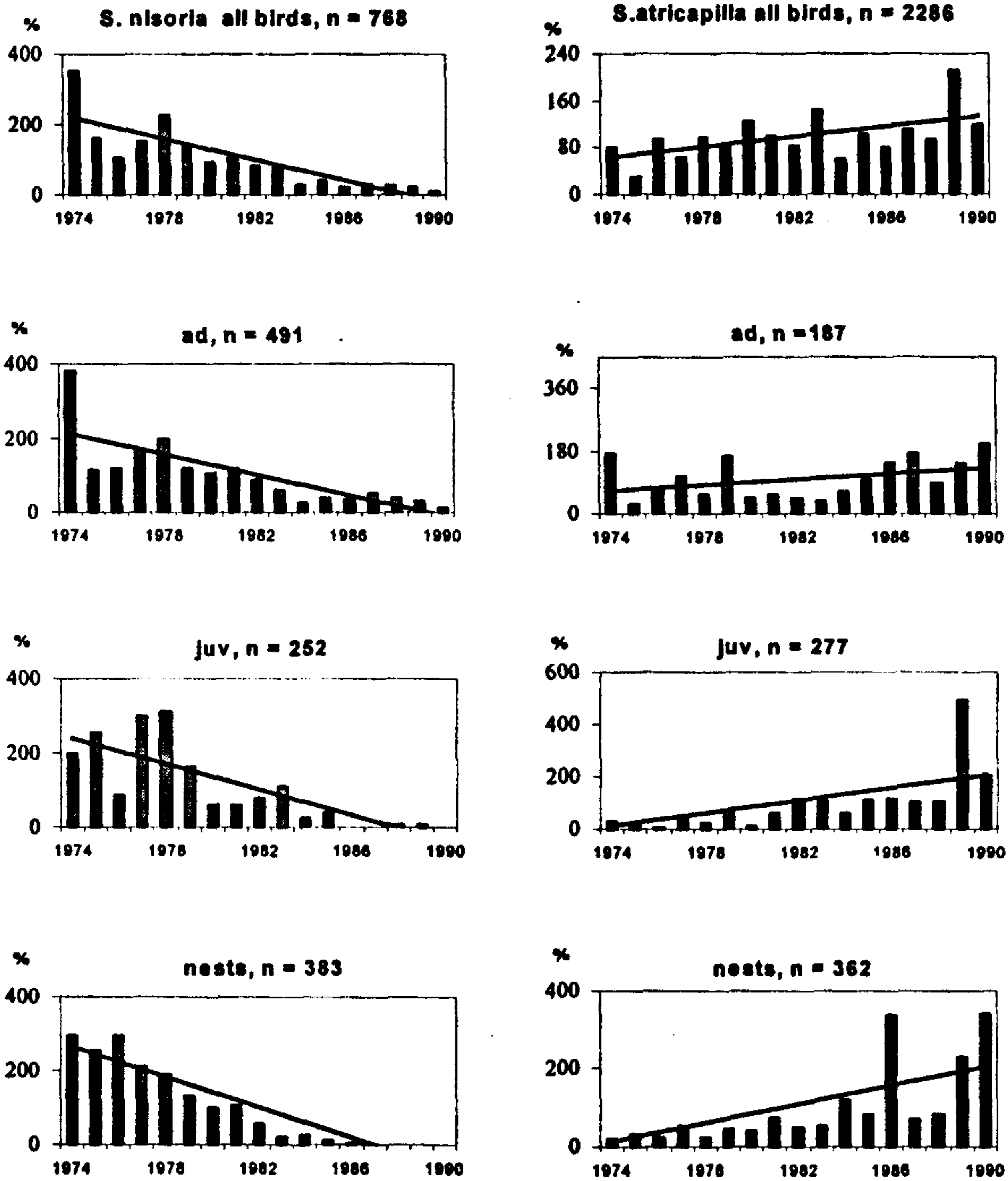

Figure 5. Opposite trends of population dynamics in the Barred Warbler and Blackcap by the trapping and nest search. For the significance of the trends **see** Tab. 11. On the Y-axis: percentage of the annual mean.

3.10. Population dynamics

Population trends of *Sylvia* warblers have been presented, along with other bird species, in many publications. For the period 1960-1976 it was shown (Dolnik & Payevsky 1979, 1982) that population trends of all birds, migrants and local breeders, varied between the species. In the Garden Warbler and Whitethroat a negative trend was recorded, in the Lesser Whitethroat a positive one, Blackcap numbers fluctuated with overall positive tendency. Barred Warbler number were growing until 1969, after which a decline was recorded. The same data supplemented until 1981 (Payevsky 1985a) showed similar trends, except for the Lesser Whitethroat in which a growth was followed by a decline since 1972. Further trapping allowed the supplementing of data on the trends until 1986 (Payevsky 1990). A negative trend was continued in the Barred Warbler, until 1984 also in the Lesser Whitethroat. In the Whitethroat, Garden Warbler, and Blackcap a positive trend was found, though significant only in summer and autumn catches, not in spring ones.

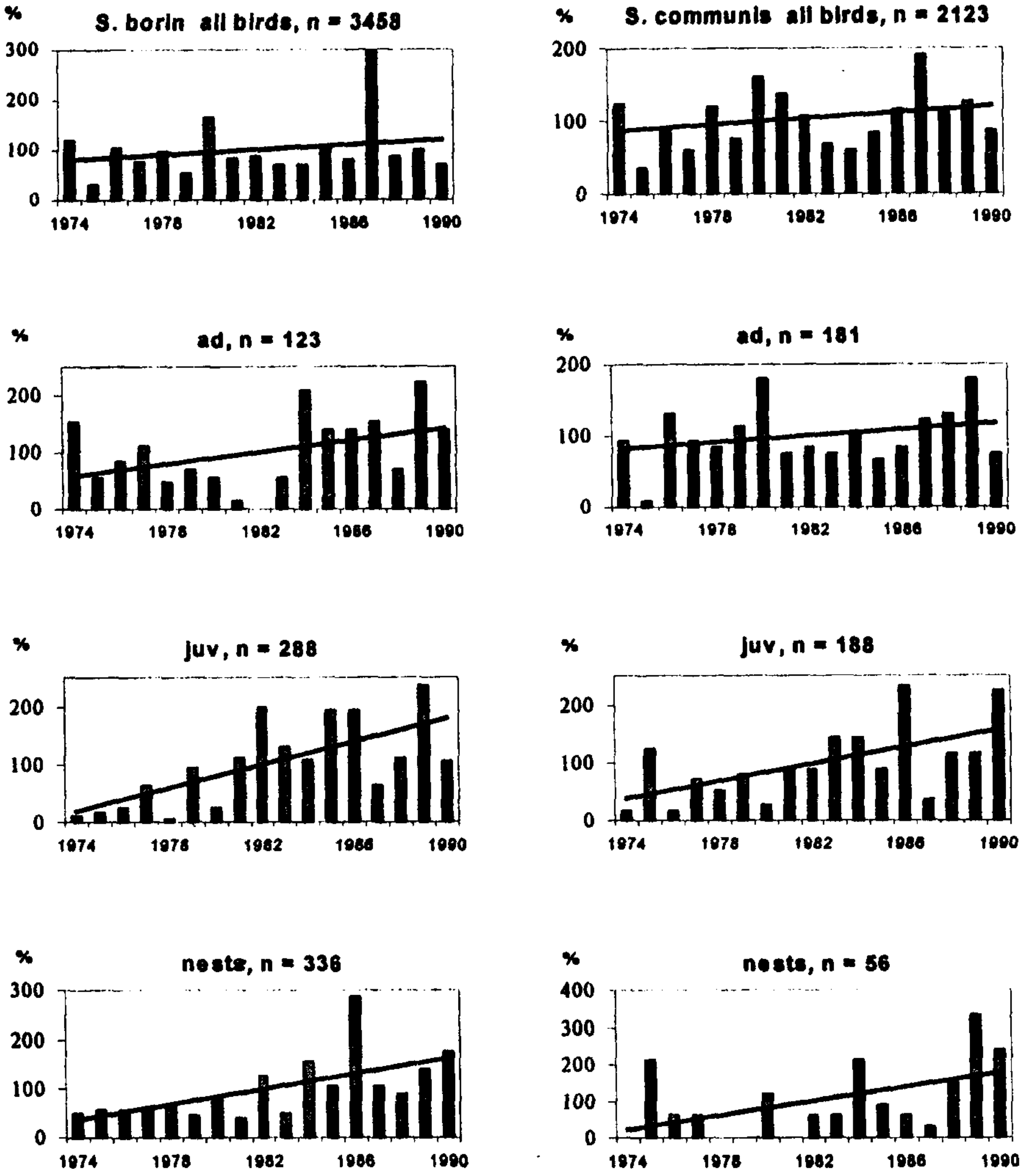

Figure 6. Population trends in the Garden Warbler and Whitethroat. For details, see legend to Fig.5.

Population trends in local *Sylvia* warblers at the study site captured only in June and July in 1959-1998 are discussed by Sokolov (in press). He shows a significant positive trend in local breeding Blackcaps and Garden Warblers in 1978-1991, a negative trend in breeding Barred Warblers in 1978-

1998, in Lesser Whitethroats in 1985-1998 and in Garden Warblers in 1959-1978 and 1985-1998. In general, numbers of *Sylvia* warblers, as in many other species, were higher in 1960s and 1980s than in 1970s and 1990s. Sokolov (in press) also shows a positive relationship between April and May temperatures and numbers of juveniles in the Blackcap, Garden Warbler, and Whitethroat, but not in the Lesser Whitethroat and Barred Warbler.

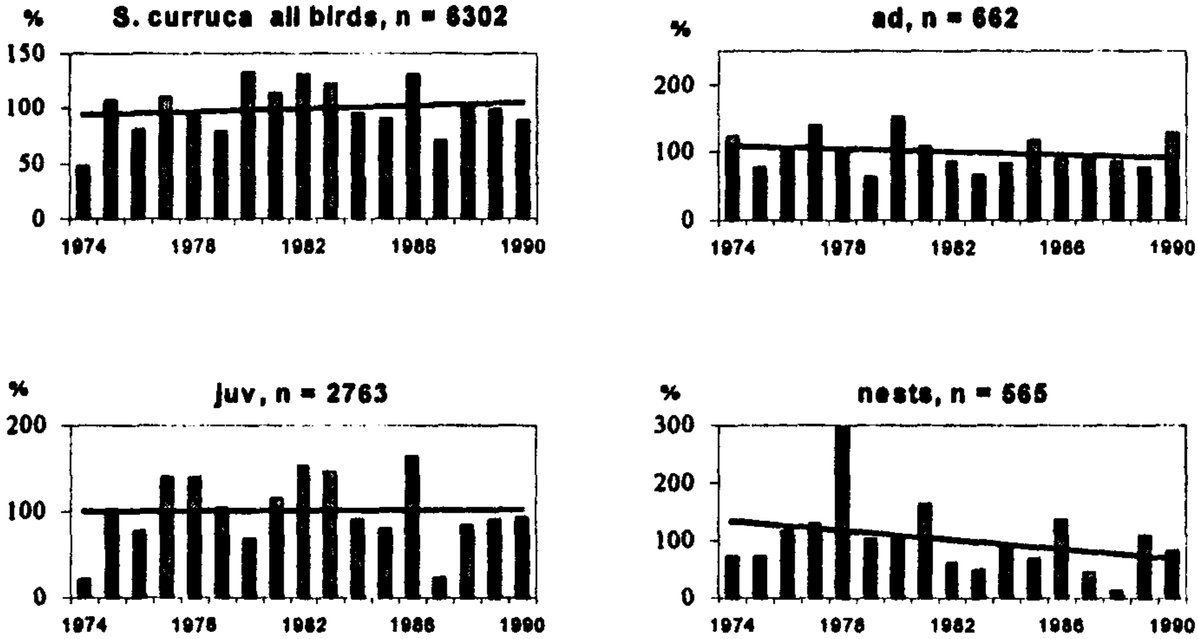

Figure 7. Fluctuations of the stable Lesser Whitethroat population. For details, see legend to Fig. 5.

I used only the data of 1974-1990 to analyse population dynamics in parallel by trapping figures and by numbers of nests found. I assume a broader time interval than Sokolov for the period when only local birds were trapped and present not absolute numbers, but percentage of mean annual numbers (Fig. 5-7). Trends were analysed by correlation of time series (one-tailed regression), and by Kendall coefficient of concordance, where one variable was the years' series, and the other - trapping figure or number of nests. Linear trends were fitted. The results are shown in Tab. 11 and Fig. 5-7. Both tests usually yielded similar results. Over the study years (1974-1990) numbers of Lesser Whitethroat were stable, whereas a dramatic decline was recorded in the Barred Warbler. A significant increase was observed in the Blackcap, Garden Warbler, and Whitethroat on the basis of numbers of juveniles trapped and nests found. In the Blackcap the increase was also confirmed by pooled trapping figures of local and migrant individuals. The most impressive result is the similarity of trends yielded by different data: by the total trapping number, by trapping of local adults, local juveniles, and by numbers of found nests.

4. Discussion

The general trends in population dynamics of *Sylvia* warblers on the Courish Spit deserves special discussion. Similar trends revealed by trapping data and by nest search, seem astonishing. Nest searches, though annual, were conducted by varying number of researchers and with different intensity. Nevertheless, both a dramatic decline, as in the Barred Warbler and a significant increase in the Blackcap were reflected by such a seemingly random variable as the number of found nests. Matching increases were also found for the Garden Warbler and Whitethroat, but were shown only by records of nests found and juveniles trapped. For fieldworkers at "Fringilla" over these years, growth of Blackcap population, nearly complete extinction of the Barred Warbler and stable numbers of the Lesser

Whitethroat were obvious without any analysis. Population trends of the Garden Warbler and Whitethroat were less obvious. I believe that the general pattern of population dynamics of the five species is evidence for the validity of the survey methods used.

Possible causes of population growth and decline in these species were discussed in a number of publications (Dolnik & Payevsky 1979, 1982, Payevsky 1985a, 1990, Sokolov 1991b, in press). Similar trends in neighbouring countries (Poland, Sweden, Denmark) showed a similar pattern of population trends in many species. The main factor which was thought to be responsible for these similar trends was environmental pollution by agricultural poisons. An analysis of trophic chains neither confirmed nor rejected their influence. It is possible that in a number of bird species years of most intensive use of DDT and other poisons in agriculture and forestry coincided with the natural decline phase of population cycles. Another aspect, inter-specific competition, is also important. A decline in a dominant species may cause a growth in competitors, for which a weaker competition appears more important than chemical pollution. On the Courish Spit the growth of the Blackcap population could be caused by the availability of territories abandoned by Barred Warblers. Moreover, these territories became more shadowed as forest grew up, and thus more suitable for Blackcaps. At any rate, in the nearest vicinity of "Fringilla" where Barred and Garden Warbler were dominating, now the most numerous species is the Blackcap. Its population may have grown both in numbers and territorially. In the 1960s it mainly bred in small isolated patches of spruce forest near the sea coast, now its nests may be found everywhere. As for the Lesser Whitethroat, its high plasticity in habitat selection provides its stable and high numbers.

A special attention should be paid to the similar habitat selection by the Barred Warbler and Red-backed Shrike. These two species usually breed in close vicinity, as reported from different regions: Leningrad Region, Russia (Malchevsky & Pukinsky 1983), Volga and Kama basin (Zatsepina 1978), NW Kazakhstan (Levin & Gubin 1985), and many western European sites (Schmidt 1981). The same pattern was observed on the Courish Spit. Drastic simultaneous decline of both populations until nearly complete extinction was at first explained only by dramatic habitat change: clearing pine plantations, cutting lower branches of Mountain Pines, cutting Barberry and Dewberry (Vinogradova 1988). However, general growing of forest coverage due to pine growth and changing structure of herbage could have detrimental impact on foraging conditions of both Red-backed Shrike and Barred Warbler (Shapoval 1988, Sokolov 1991b). Many authors discussed possible causes of Red-backed Shrike decline in Europe (Lefranc 1973, Anonymous 1985, Wassmann 1986, Kowalski 1987, Olsson 1995, etc.). However, no publications discussing the causes of similar habitat selection by Red-backed Shrikes and Barred Warblers are available. In a chapter devoted to this issue, Schmidt (1981) summarizes the following data on interrelations of these species. They do not compete for food, as they utilise different prey. Shrikes do not attack Barred Warbler's nestlings, no aggressive behaviour is recorded between these species. They usually built nests at different heights. Thus, it is only similar habitat selection which is in common. Red-backed Shrikes may also serve as additional defence for Barred Warblers, as strong defensive behaviour is typical for shrikes in dangerous situations.

In the very recent years, 1997-1998, Red-backed Shrike population probably started to recover (several nests were found). As already mentioned, in 1997 two breeding attempts were recorded in the Barred Warbler, thus a new population increase may be expected.

Parallel changes in numbers of local and passage birds are difficult to interpret. On the one hand, factors causing population change act over large areas, influencing breeding areas, migratory routes, and winter quarters. Global climatic change may be such a factor. In some parts of the continent inter-annual fluctuation of spring and summer temperatures may play a role (Sokolov, in press). With this in mind all attempts to explain population dynamics by local factors (i.e. forest clearance, chemical pollution, local weather events) lose credibility. Recently revealed dynamics of *Sylvia* numbers in 1961-1990 derived from trapping data from 14 stations in Sweden, Finland, Estonia, Latvia, Poland, Germany, and from our data (Busse et al. 1995), fits our pattern of inter-specific variation only partly. In this publication autumn trapping figures of all *Sylvia* species are reported to decrease over the study years, the decrease being most evident in the Barred Warbler and least evident in the Blackcap. Thus, the pan-European trend is similar to our data for the Barred Warbler only, and the difference between the Barred Warbler and the Blackcap is the greatest in both data sets. It is noteworthy that the trapping pattern at Ottenby, Sweden (Pettersson 1989) is most similar to our data from the Courish Spit.

Other results for the greater part support the findings for some other populations. Timing of migration on the Courish Spit was similar to that in the western Baltic at Ottenby on Oland (Enquist & Pettersson 1986). In Britain *Sylvia* warblers arrive in spring 2-3 weeks earlier than in the Baltic area (Fransson 1995) and breeding starts correspondingly earlier (Mason 1976, Boddy 1993). Size and body mass of Courish warblers were within the recorded values of European populations (Eck 1990, Cramp et al. 1992). The same applies to clutch size and some other life traits that did not differ from patterns reported from different European and Asian sites: England (Mason 1976), Central and Northern Europe (Bairlein et al, 1980, Neuschuiz 1981), Finland (Solonen 1979), NW Russia (Zimin et al. 1978), Leninigrad Region (Russia) (Muzayev 1980, Malchevsky & Pukinsky 1983), Volga and Kama basin (Russia) (Zatsepina 1978), Western Siberia (Gureyev & Milovidov 1983) and NW Kazakhstan (Levin & Gubin 1985).

Breeding success calculated after the traditional method (not after Mayfield) was in the Blackcap the same as in Pskov Region (Russia) (Bublichenko & Fetisov 1989) but slightly higher than in some European sites (Berthold et al. 1990). Breeding success in Barred Warbler was higher than in Northern Germany (Neuschuiz 1981). In the Lesser Whitethroat breeding success was exactly the same as in SE England (Mason 1976) and on southern Ladoga shore in NW Russia (Muzaev 1981). Annual survival in this species also did not differ from values reported from England (Boddy 1994).

Some life traits differed significantly over the study period. One may speculate that changes of wing length and body mass could have been related to population trends; Blackcap population growth was associated with an increase in body mass, and the decline of the Barred Warbler was associated with a decrease in wing length in females. However, conclusions are difficult, as size trends were recorded in females only and were not related to each other (i.e. wing chord did not vary in accordance with body mass). Size trends in the Garden Warbler and Whitethroat, though significant, were very small and do not probably deserve a serious discussion.

Rising proportion of Blackcap and Garden Warbler nests built on Red Currant and declining proportion of all nests on pine in 1981-1995 compared to previous years was undoubtedly caused by the local forestry management who cleared pine forest and cut off lower branches in both Scots and Mountain Pine. Warblers that occupied breeding territories on the edges of pine forest did not have to use pines for nest construction. This also caused an increased proportion of Lesser Whitethroat's nests on Juniper, and declining average height of nests position in this species. As for rising height of Barred Warblers' nests location over the study period, it could have been caused by the growth of pine plantations where 30% of the population nested. A closer examination, however, did not confirm this relationship.

Variation in clutch size and breeding success (Tab. 9) could be related to long-term fluctuations of spring temperatures. Elsewhere (Sokolov & Payevsky 1998) has shown that higher temperatures in April and in May in the 1960s and 1980s compared to the 1970s and 1990s caused earlier breeding in many bird species, including *Sylvia* warblers. One may suggest that larger clutches and higher breeding success in the 1960s and 1980s were also caused by more supportive breeding conditions in warmer seasons. Sokolov (in press) found a positive relationship between spring temperatures and numbers of juvenile warblers, but only in three species, excluding the Barred Warbler and Lesser Whitethroat. In these species nests are better concealed (up to 59% of Lesser Whitethroat's nests are built on Juniper and Mountain Pine; up to 40% of Barred Warbler's nests are found on low Mountain Pine bushes) which could lead to a weaker dependence between breeding success and ambient temperature (Tab. 9). This can also explain the lack of inter-annual variation in productivity of these populations, i.e. lower impact of the weather on their abundance.

Maximal age recorded in three warbler species in this study was achieved only be males. This is in accordance with our results concerning age-specific survival in birds. As opposed to other animals, higher survival in male birds is recorded significantly more frequently than in females (Payevsky et al. 1997).

All factors, both human-induced and natural, can probably influence populations dynamics of birds, incl. *Sylvia* warblers. A complex pattern of interplay of these factors in different geographic regions may cause similar or varying population trends. The idea to isolate a single most important factor responsible for all variation observed done not seem productive.

A conclusion may be drawn that detailed long-term population projects on well-studied species may bring new aspects to our knowledge and open new study directions.

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